

Reproductive migration of the coconut crab *Birgus latro*

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Abstract: Knowledge of movement patterns is essential in tailoring spatial conservation and management measures. Although populations of the coconut crab, *Birgus latro*, have been severely depleted in most habitats, there have been few serious attempts to manage the resources. Recently, spatial conservation (e.g. seasonal area closure) has been suggested as an effective tool for resource management. However, relatively little is known about coconut crab movements, especially reproductive migration. To determine the dynamics of the reproductive migration of coconut crabs, we investigated both male and female migration patterns during the reproductive season in Hatoma Island, southwest of Japan. Both females and males migrated between inland and coastal areas during the reproductive season. Observed female seaward and landward migrations were temporally coincident with their reproductive activities (egg extrusion and larval hatching). Observed temporal-spatial distribution of males would be shaped by temporal variations in expected future mating opportunities within the reproductive season and male reproductive strategy in response to these variations.

Key words: *Birgus latro*, coconut crab, reproduction, reproductive migration, seasonal area closure

Introduction

The value of area closure as a conservation management tool depends on the movement pattern of target species. Knowledge of movement patterns is central in determining a population's response to spatial protection (Guénette & Pitcher 1999) and is essential in tailoring spatial conservation and management measures (Meyer et al. 2007). Seasonal area closure, one type of area closure, can be highly useful in protecting target species from mortality at a specific stage of its life history, for example during reproduction (e.g. Beets & Friedlander 1999). Seasonal area closure centered around the reproductive season of target species not only reduces human exploitation of their resources but also removes disturbances to the breeding population at a critical phase in their life cycle.

The coconut crab *Birgus latro* (Linnaeus 1767) lives in coastal areas of tropical Indo-Pacific regions. Populations in most habitats have been severely depleted or have become virtually extinct (Brown & Fielder 1991), due primarily to overharvesting (Fletcher 1993) and habitat de-

struction (Eldredge 1996). The coconut crab was listed as vulnerable in 1981 on the IUCN Red List. In 1996 the listing was downgraded to the data deficient category, not because the species had recovered but because of the lack of available data (Eldredge 1996). Although coconut crabs have been traditionally eaten by locals, there have been few serious attempts to manage the stocks of this species in most regions (Fletcher 1993).

In recent years, the coconut crab populations in the Sakishima archipelago, southwest of Okinawa, Japan, have decreased dramatically (Shokita 2006). Since 2010, minimum legal size limits, seasonal closures, and a ban on the capture of ovigerous females have been enforced in Tarama Island, one of the islands in the archipelago, as first steps in conserving coconut crab resources in Japan. In addition, spatial conservation, including sanctuary (no-take zones) and/or seasonal area closure, has been suggested as an effective tool for resource management (Sato 2011a, Sato 2012).

Relatively little is known about coconut crab movement, especially reproductive migration, but such knowledge is essential to justify establishment of seasonal area closure with the aim of avoiding human disturbance of their repro-

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ductive activities. According to Schiller et al. (1991), only female coconut crabs participate in reproductive migration, with no male crabs migrating for reproductive purposes. That study suggested that, starting approximately 4–5 weeks prior to larval releasing, females migrate from inland areas to the coast to release larvae into the ocean. Shortly after arriving on the coast, females extrude eggs. Soon after releasing their larvae, the females return to inland areas. Despite this hypothesis, however, there are no published data providing accurate information on coconut crab reproductive migrations. There is the need for further research to accurately determine the dynamics of reproductive migration (Drew et al. 2010). So the aim of the present study was to investigate both male and female migration patterns during the reproductive season in order to determine the dynamics of reproductive migration in the coconut crab.

Materials and Methods

Both male and female distributions during the reproductive season were investigated by field observations on Hatoma Island (24°28'N, 123°49'E), one of the islands in the Sakishima archipelago, located southwest of Okinawa, Japan. This island has an area of 0.96 km² and is approximately 4 km in circumference, and the coconut crab reproductive season starts around early June and ends in late August, although most females finish extruding eggs by mid-July (Sato & Yoseda 2008).

To determine their landward and seaward migrations, crabs were captured by hand in two areas, one inland and one coastal area, at night (19:30–24:00) between 2 June and 28 August at intervals of approximately 7 d in 2007. Collection at the inland and coastal areas was performed simultaneously by two researchers working independently, one at each site. The inland area is located at least 260 m from the shoreline and is characterized dense vegetation. The coastal area is adjacent to the sea and is characterized by jagged limestone pinnacles.

Captured crabs were sexed according to the presence of pleopods on the left ventral surface: only females have pleopods, which support their eggs externally (Fletcher 1993). The thoracic length (TL) of each crab was measured to the nearest 0.1 mm using Vernier calipers (Mitutoyo Corporation, CD-20PM). The sizes of 50% sexual maturity were estimated as 22.2 mm TL in males (Sato et al. 2008) and 24.5 mm TL in females (Sato & Yoseda 2008), so males and females below these respective sizes were excluded from the study. Captured crabs were released immediately just after the observations. The carapace of each captured individual was marked with paint before the release to avoid duplicate specimen counts.

The reproductive condition of each female was recorded; that is whether they were non-ovigerous, ovigerous (with eggs), or had already released larvae, with the latter indicating by the egg membranes of hatched embryos at-

tached to the pleopods. Females extrude only one clutch per reproductive season (Sato & Yoseda 2008), so non-ovigerous females were defined as pre-egg-extruding individuals. However, in some females, the eggs may have been released early in the reproductive season, with all egg membranes decaying completely by late August, thus making it difficult to distinguish between pre-egg-extruding (non-ovigerous) and post-releasing females. Pleonal expansion (PE) was therefore measured for non-ovigerous females without egg membranes captured in August. Coconut crabs have four tergites, and the distance between the tergites increases when the pleon becomes enlarged. Distances between second and third tergites (A) and between third and fourth tergites (B) were measured to calculate the PE using the formula $PE=(A+B)/TL$ (Sato & Yoseda 2009b). The PE index strongly correlates with female reproductive status during the reproductive season (Sato & Yoseda 2009b). The PE decreases markedly after egg extrusion, remaining until the end of the reproductive season; with the mean \pm SD of pre-egg-extruding females, ovigerous females, and post-releasing females being 0.24 ± 0.15 ($n=226$), 0.02 ± 0.06 ($n=120$), and 0.04 ± 0.09 ($n=102$), respectively (Sato, unpubl. data). Therefore, any female without eggs or egg membranes and a $PE < 0.04$ was defined as a post-releasing females.

The numbers of individuals captured in each area were compared using the *G* test (null hypothesis 50 : 50, $\alpha=0.05$) for each sex. Williams' correction was used because it provides a better approximation of the chi-squared distribution than unadjusted *G* statistics, and is a more conservative test with a lower sample size (Sokal & Rohlf 1981). The proportions of males and females captured in the coastal area, defined as the number captured in the coastal area as a fraction of the total number captured in both areas, were compared with Fisher's Exact Test to determine whether habitat use of coconut crabs varies temporally between sexes.

Results

Sex difference in temporal-spatial distribution

A total of 424 mature males and 480 mature females were captured in the two areas throughout the field investigations. Both females and males were distributed throughout the inland and coastal areas during the reproductive season (Figs. 1a–c). The number of males captured in the coastal area dropped sharply on 22 July, and significant differences between areas in the number of captured males were observed from late July through early August (*G* test, 22 July, $G_{adj, 1}=12.7$, $p<0.001$; 30 July, $G_{adj, 1}=14.5$, $p<0.001$; 6 August, $G_{adj, 1}=17.1$, $p<0.001$; Fig. 1a). During the first half of the reproductive season, until mid-July, however, more males were captured in the coastal than in the inland area, although the differences were not significant.

In contrast to males, the numbers of females captured in

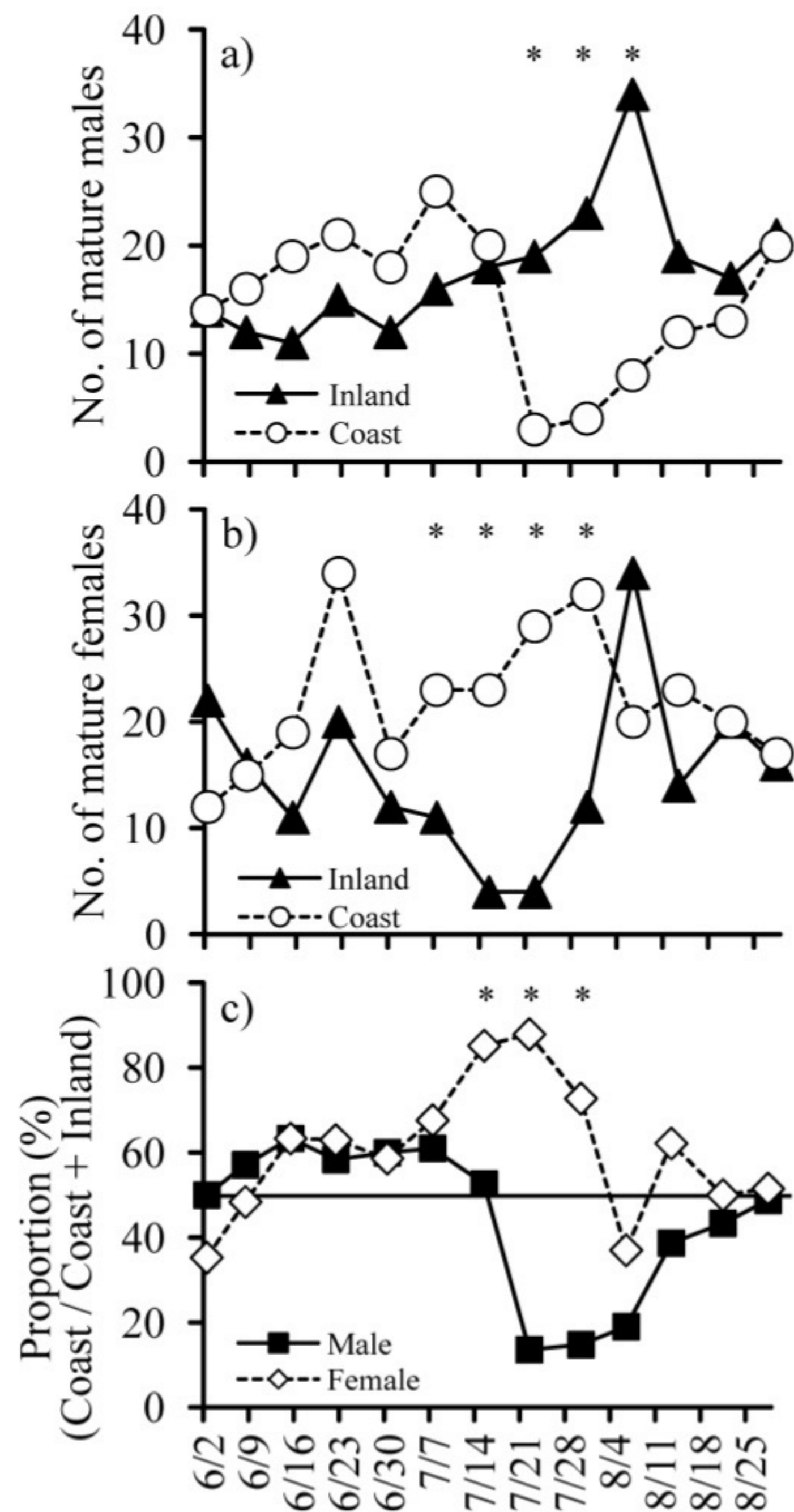


Fig. 1. Temporal changes in the number of mature male (a) and female (b) coconut crabs in inland and coastal areas, and (c) temporal variations in the proportions of individuals of each sex in the coastal area during the reproductive season. The asterisks indicate significant difference.

the coastal area were significantly higher throughout July (G test, 7 July, $G_{adj, 1}=4.3$, $p=0.039$; 15 July, $G_{adj, 1}=14.5$, $p<0.001$; 22 July, $G_{adj, 1}=21.0$, $p<0.001$; 30 July, $G_{adj, 1}=9.3$, $p=0.002$; Fig. 1b). Therefore, significant gender related differences in habitat use were observed during middle to late July (Fisher's Exact Test, 15 July, $p=0.008$; 22 July, $p<0.001$; 30 July, $p<0.001$; Fig. 1c).

Relationships between female distribution patterns and reproductive conditions

Female temporal-spatial distribution patterns varied with their reproductive conditions (Figs. 2a–d). The numbers of pre-egg-extruding females captured in the inland and coastal areas were almost equivalent (Fig. 2a), and then the proportion of pre-egg-extruding females continued to decrease as the reproductive season progressed (Fig. 2d). In contrast, most ovigerous females were captured in the coastal area (Fig. 2b), and the proportion of ovigerous females peaked around the middle of July (Fig. 2d). In mid-July to early August, the number of post-releasing females increased first in the coastal area, followed approxi-

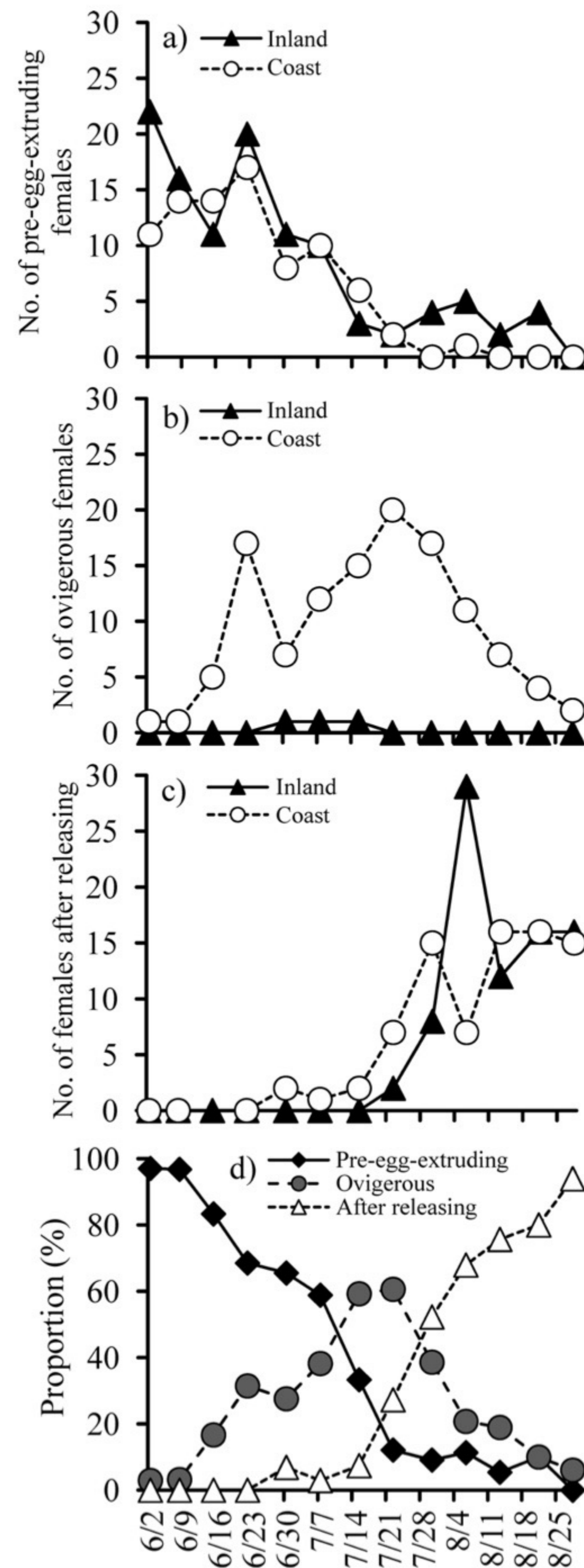


Fig. 2. Temporal variations in the numbers of mature pre-egg-extruding (a), ovigerous (b), and post-releasing females (c) in inland and coastal areas, and (d) temporal variations in the number of mature females of each reproductive condition observed on Hatoma Island during the reproductive season.

mately 7 days later by an increase in the inland area (Fig. 2c).

Discussion

Causes of the female temporal-spatial distribution

Temporal-spatial distribution during the reproductive season differed between sexes. Observed female distribution patterns are presumably would be related to female re-



Fig. 3. Photograph showing a pair of coconut crabs in the course of mating- July 10, 2008, at 1927, Hatoma Island.

productive condition. Although the numbers of pre-egg-extruding females captured in the inland and coastal areas were almost equal, few ovigerous females were captured in the inland area (Fig. 2b), supporting the hypothesis that, just before egg extrusion, pre-egg-extruding females migrate from inland to coastal areas, extruding eggs shortly thereafter (Schiller et al. 1991). Sato & Yoseda (2009a), too, concluded that egg extrusions occur near the coastal area based on a direct observation of egg extrusion. In addition, a sequence of mating behavior of coconut crab pair was observed approximately 30 m from the shoreline of Hatoma Island in July 2008 (Fig. 3), in agreement with previous observation (Helfman 1977). Mating of this species is followed within <1 week by egg extrusion (Sato & Yoseda 2009b), suggesting that both mating and egg extrusion occur near the coast.

In this species, the period of egg incubation, from egg extrusion to larval release, has been estimated at about 25 to 45 days, with the majority of the period of egg incubation 27–29 days (Schiller et al. 1991). During the period of egg incubation, the coastal area would be a suitable habitat for ovigerous females because of seawater requirements for egg incubation; the susceptibility of eggs to inundation by water and exposure to desiccating conditions; and for the purpose of releasing larvae into the ocean (Schiller et al. 1991). Therefore, just before egg extrusion, pre-egg-extruding females would migrate from inland to coastal areas, and the distribution of ovigerous females was extremely biased toward the coastal area (Fig. 2b).

After releasing larvae, around middle July to early August, females started their landward migration. The number of post-releasing females increased first in the coastal area, followed by an increase in the inland area (Fig. 2c). Schiller et al. (1991) suggested females depart the coast and return inland approximately 4–10 days after releasing their larvae. In the inland area, coconut crabs were ob-

served to feed on the fruits of various plants, e.g. *Alocasia odora*, *Diospyros ferrea*, *Ficus septica*, *F. microcarpa*, *Livistona chinensis*, *Macaranga tanarius*, and *Pandanus odoratissimus*, and on insects such as the blackish cicada, *Cryptotympana facialis*, and the grasshopper, *Isopsera denticulata* (Sato, unpubl data). In the coastal area, however, few crabs were observed to participate in feeding activity, although some individuals fed on exuvia of the shore crab, *Grapsus albolineatus*. These findings suggest that the inland area is a more suitable feeding habitat for this species than the coastal area, with the former having a more plentiful food supply. Therefore, following the long period of egg incubation in the coastal area, females presumably leave for the inland area immediately after releasing larvae, resulting in no significant difference in female habitat use after early August (Fig. 1c).

The observed female seaward and landward migrations were temporally coincident with their reproductive activities (egg extrusion and larval releasing), indicating that the observed temporal-spatial distribution of females was caused by female reproductive migration.

Causes of the male temporal-spatial distribution

The observed male temporal-spatial distribution pattern would be influenced by the female reproductive migration. Sato (2012) reviewed a part of reproductive ecology of coconut crab. During mating, males deposit a spermatophore mass over and near the gonopores on the female ventral surface because females have no spermatheca, and the time lapse between mating and egg extrusion is estimated to be less than 1 week. While females extrude only one clutch in a reproductive season, males can have several matings with females within a reproductive season. However, as the reproductive season progressed, the proportion of pre-egg-extruding females, constituting the potential number of mates for males, continued to decrease, with most females having finished mating and egg-extrusion early in the reproductive season (Fig. 2d). The opportunity for further matings for males dropped sharply by 22 July, becoming negligible later in the season. If matings, as well as egg extrusion, of this species occur near the coastal area, males would be expected to stay in coastal areas to improve their chances of meeting and mating with pre-egg-extruding females early in the reproductive season, even if the coastal area is not a suitable habitat with respect to food supply. More males were observed in the coastal than in the inland area until mid-July, although the difference was not statistically significant (Figs. 1a, c).

On 22 July, the proportion of males captured in the coastal area suddenly dropped, indicating that many males had started to migrate from the coastal to the inland area between 15 and 22 July in advance of the female landward migration (Fig. 1c). The start of male landward migration was temporally coincident with the disappearance of the opportunity for further matings, indicating that most males had finished their reproductive activities by 22 July. It has

been shown that about 50% of males on this island have depleted their sperm reserves by late June (Sato 2011b). The frequency of male encounters with pre-egg-extruding females near the coastal area may provide information on future mating opportunities for males. The male landward migration after mating activity may be related to the plentiful food supply in the inland area.

The male temporal-spatial distribution during the reproductive season would be shaped by temporal variations in expected future mating opportunities within the reproductive season and male reproductive strategy in response to these variations. The significant differences in temporal-spatial distribution between the sexes (Fig. 1c) can be explained by the female requirement to spend a longer period of time in the coastal area than males for egg incubation and larval releasing.

After the male landward migration, the number of males captured in the coastal area increased gradually throughout August and then became nearly equal to that in the inland area at the end of the field investigation (Fig. 1a). Also at the start of the investigation, the number of males captured in each area was approximately equal. Such a spatial distribution pattern was observed also in females (Fig. 1b) and might be expected outside the reproductive season because coconut crabs must haunt coastal area to drink sea water for maintenance of their osmotic balance (Gross 1955, Fletcher 1993, T. Sato, personal observation).

Resource management

To our knowledge, this is the first report to address the occurrence of male reproductive migration and the dynamics of reproductive migration in the coconut crab. Our findings may contribute to the establishment of seasonal area closures, removing human disturbances of crab reproductive activities. The male and female reproductive migrations between the coastal and inland areas indicate that it is important not only to conserve both habitats but also to keep the connectivity between the habitats within seasonal area closure for sustaining their egg production and recovering coconut crab resources. Of course, seasonal area closures should include sites near coastal areas in which reproductive activities (mating, egg extrusion and larval releasing) occur, thus removing human disturbances of breeding populations. Although slot size limits with male-only harvesting (Sato & Yoseda 2010, Sato et al. 2010, Sato & Suzuki 2010) and seasonal closure (Sato & Yoseda 2009b) have been recommended to maintain the optimal reproductive rate of coconut crab resources, combinations of various management measures should also be considered (Sato 2012), including the conservation of suitable habitats in order to optimize the maintenance of target—(in this case, coconut crab—) resources (see for example Jack & Wing 2010).

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References

- Beets J, Friedlander A (1999) Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environ Biol Fish* 55: 91–98.
- Brown IW, Fielder DR (1991) Project Overview and Literature survey. In: *The Coconut Crab: Aspects of Birgus latro Biology and Ecology in Vanuatu* (eds Brown IW, Fielder DR). ACIAR Monograph 8, Canberra, pp. 1–11.
- Drew M, Harzsch S, Stensmyr M, Erland S, Hansson BS (2010) A review of the biology and ecology of the robber crab, *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae). *Zool Anz* 249: 45–67.
- Eldredge LG (1996) *Birgus latro*. In: IUCN Red List of Threatened Species (ed IUCN 2012). Available at: www.iucnredlist.org/details/2811/0. (accessed on 13 August 2012)
- Fletcher WJ (1993) Coconut crabs. In: *Nearshore marine resources of the South Pacific* (eds Wright A, Hill L). University of the South Pacific, FFA, and ICOD, Suva, pp. 643–681.
- Gross WJ (1955) Aspects of osmotic regulation in crabs showing the terrestrial habit. *Am Nat* 89: 205–222.
- Guénette S, Pitcher TJ (1999) An age-structured model showing the benefits of marine reserves against overexploitation. *Fish Res* 39: 295–303.
- Helfman GS (1977) Copulatory behavior of the coconut or robber crab *Birgus latro* (L.) (Decapoda, Anomura, Paguridea, Coenobitidae). *Crustaceana* 33: 198–202.
- Jack L, Wing SR (2010) Maintenance of old-growth size structure and fecundity of the red rock lobster *Jasus edwardsii* among marine protected areas in Fiordland, New Zealand. *Mar Ecol Prog Ser* 404: 161–172.
- Meyer CG, Holland KN, Papastamatiou YP (2007) Seasonal and diel movements of giant trevally *Caranx ignobilis* at remote Hawaiian atolls: implications for the design of Marine Protected Areas. *Mar Ecol Prog Ser* 333: 13–25.
- Sato T (2011a) Coconut crab resource management based on reproductive ecology. *Cancer* 20: 87–92. (In Japanese)
- Sato T (2011b) Plausible causes for sperm-store variations in the coconut crab *Birgus latro* under large selective harvesting. *Aquat Biol* 13: 11–19.
- Sato T (2012) Impacts of large male-selective harvesting on reproduction: Illustration with large decapod crustacean resources. *Aqua-BioSci Monogr* 5: 67–102.
- Sato T, Suzuki N (2010) Female size as a determinant of larval size, weight, and survival period in the coconut crab, *Birgus latro*. *J Crust Biol* 30: 624–628.
- Sato T, Yoseda K (2008) Reproductive season and female matu-

- rity size of coconut crab *Birgus latro* in Hatoma Island, southern part of Japan. *Fish Sci* 74: 1277–1282.
- Sato T, Yoseda K (2009a) Egg extrusion site of coconut crab *Birgus latro*: direct observation of terrestrial egg extrusion. *Mar Biodivers Rec* 2: e37.
- Sato T, Yoseda K (2009b) Prediction of timing of mating and egg extrusion in the coconut crab *Birgus latro* judged from female pleonal expansion. *Fish Sci* 75: 641–648.
- Sato T, Yoseda K (2010) Influence of size- and sex-biased harvesting on reproduction of the coconut crab *Birgus latro*. *Mar Ecol Prog Ser* 402: 171–178.
- Sato T, Yoseda K, Abe O, Shibuno T (2008) Male maturity, number of sperm and spermatophore size relationships with male size in coconut crab *Birgus latro* in Hatoma Island, southern part of Japan. *J Crust Biol* 28: 663–668.
- Sato T, Yoseda K, Okuzawa K, Suzuki N (2010) Sperm limitation: possible impacts of large male-selective harvesting on reproduction of the coconut crab *Birgus latro*. *Aquat Biol* 10: 23–32.
- Schiller C, Fielder DR, Brown IW, Obed A (1991) Reproduction, early life-history and recruitment. In: *The Coconut Crab: Aspects of Birgus latro Biology and Ecology in Vanuatu* (eds Brown IW, Fielder DR). ACIAR Monograph 8, Canberra, pp. 13–35.
- Shokita S (2006) Coconut crab. In: *Red Data Book on Crustaceans* (ed Nature Conservation Bureau, Japan Ministry of the Environment). Japan Wildlife Research Center, pp.54. (In Japanese)
- Sokal RR, Rohlf FJ (1981) *Biometry: The Principles and Practice of Statistics in Biological Research*, 2nd edition. WH Freeman, New York, 859 pp.